

EFFECTS OF ACIDIFYING ENVIRONMENTS ON FRESHWATER MOLLUSKS IN SOUTHERN ONTARIO, CANADA

G. L. MACKIE

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GUELPH
GUELPH, ONTARIO, CANADA N1G 2W1

ABSTRACT

Laboratory and field studies on freshwater Mollusca in several low-alkalinity lakes of south-central Ontario indicate that neither the hydrogen ion concentration nor the metal (cadmium, lead, aluminum) concentrations in the lake are lethal as independent or joint toxicity factors. However, changes in the calcareous composition of the shell and changes in shell morphometry can be related to low alkalinity and/or pH of the environment. These changes are accompanied by decreased growth and reproduction that have depressed the production and species diversity of the molluscan communities. As lakes acidify, the epifaunal grazers (gastropods) in the molluscan community are replaced by in-faunal filter feeders (Pisidiidae). The mollusks can play an important role in the sources and cycling of carbonates in acidifying environments.

Considerable research has been completed in the last decade on the effects of acidifying environments on freshwater mollusks, especially in Scandinavia (J. Økland, 1969; 1980; Økland and Økland, 1980; K. Økland, 1979, 1980; Økland and Kuiper, 1980) and Canada (Mackie and Flippance, 1983a, b, c; Rooke and Mackie, 1984a, b, c; Servos *et al.*, 1985). These studies have demonstrated direct and indirect effects of low alkalinity environments on mollusks at both the population and community levels (Fig. 1). Although most studies have examined molluscan responses to acidifying environments, evidence indicates that mollusks may alter the response of low-alkalinity lakes to additions of acid precipitation. This paper summarizes the responses of mollusks in low-alkalinity environments in southern Ontario to additions of acid and the possible effects that mollusks may have on their freshwater milieu.

DIRECT EFFECTS

HYDROGEN ION TOXICITY

High hydrogen ion concentration is lethal to most mollusks. However, each molluscan species has its own median level of tolerance to hydrogen ion concentration (Mackie, 1986). A survey of the literature cited above shows that certain Pisidiidae [e.g. *Pisidium casertanum* (Poli)] are among the last mollusks to disappear from acidifying lakes, suggesting that they should be more tolerant of high hydrogen ion concentration than other freshwater mollusks. Indeed, 96 hr static laboratory bioassays with 10 clams of each species

held at 5 pH levels (2.0, 3.0, 4.0, 5.0, 6.0 and a control at pH 7.0) using sulfuric acid (additional methods given in Mackie, 1986), have shown a decreasing order of tolerance in adult *P. casertanum* (LC50 pH = 2.7), *Musculium securis* (Prime) and *Amnicola limosa* (Say) (LC50 pH = 3.0), *Pisidium compressum* Prime (LC50 pH = 3.3), and *Sphaerium striatinum* (Lamarck) and *Valvata tricarinata* (Say) (LC50 pH = 3.5). In the Pisidiidae, the larval stages appear to be more tolerant than the adults to hydrogen ions (Mackie *et al.*, 1983), but in the Hydrobiidae the embryonic stages are much more sensitive than the adults (Servos *et al.*, 1985).

Although excess hydrogen ions are toxic to mollusks, none of the acidifying lakes studied in Ontario, Canada, have hydrogen ion concentrations that exceed the LC50 values found in the laboratory bioassays (Mackie, 1986). This includes the short term pH depressions that occur in the spring in most low-alkalinity lakes (pH = 4.5; Servos, 1983). Therefore, the disappearance of molluscs from acidifying lakes in southern Ontario is not likely due to lethal concentrations of hydrogen ions *per se*. Jewell (1922) concluded that substrate type was a more important variable than pH in determining the distribution of Unionidae in a slightly acidic (pH 5.8 - 7.1) stream in Illinois, and Fuller (1974) and Harman (1974) discuss several variables, including pH and alkalinity, that limit the distribution of mollusks.

Harman (1969) implied that changes in pH in poorly-buffered streams of New York may be at least partially responsible for the eradication of some Unionidae. However, the response of mollusks to acidity may depend on the time of

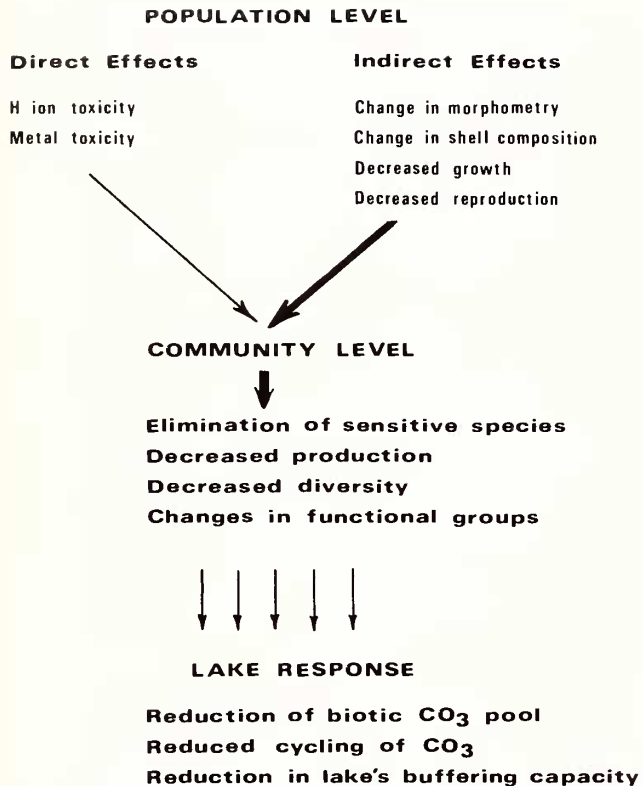


Fig. 1. Summary of direct and indirect effects of acidifying environments on freshwater mollusk communities and the response of low-alkalinity lakes as a result of these effects. Thicker arrows indicate greater effects than thin arrows.

year and/or their level of activity. For example, studies by Servos (1983) showed that many mollusks are inactive or in a dormant state during spring pH depression events, and even if the pH is artificially dropped from 5.5 to 3.5 there is little or no mortality of adult mollusks during these short periods (i.e. hours) of large pH variations. On the other hand, when Matteson (1955) transplanted mussels into lake waters of pH 4.4 - 6.1 for about six weeks during the growing season (June to August), the response of the mussels toward acidity was similar to those toward estivation (i.e. the valves clamp shut, the body-parts decrease in volume, the pH of mantle fluids drop, and all movements cease). Moreover, not all mussels seem to have the same sensitivity or response to low pH; Morrison (1932), Buckley (1977), and Mackie and Flippance (1983c) reported mussels living throughout a broad range (5.50 - 8.63) in pH, with *Elliptio complanata* (Lightfoot, 1786) itself occurring over the entire range.

METAL ION TOXICITY

An increase in hydrogen ion concentration in lakes is usually accompanied by an increase in concentrations of metals, especially cadmium, aluminum, zinc, and lead (Wurtz, 1962; LaZerte, 1984; Moore and Ramamoorthy, 1984). These

Table 1. 96 hr LC50 values (mg l⁻¹) of three metals at pH 4.0 for adults of three species of freshwater mollusks.

SPECIES	Cadmium	Lead	Aluminum
<i>Pisidium casertanum</i>	0.50	16.2	>0.400
<i>Pisidium compressum</i>	0.70	30.8	>0.400
<i>Amnicola limosa</i>	1.20	21.0	>0.400

metals are toxic to mollusks (Wurtz, 1962; Mackie, 1986), and if present in high enough concentrations, will directly eliminate them from contaminated lakes. Mackie (1986) found *Pisidium casertanum* to be more tolerant of Cd, Al, and Pb than *Amnicola limosa* (Table 1). However, the LC50 values for each metal is at least an order of magnitude greater than has been measured in any of the acidifying lakes in Ontario (Mackie, 1986). Moreover, the metals (Al, Cd, and Pb) used in the laboratory bioassays were mainly in the inorganic forms which are more toxic than the organic forms that dominate most low-alkalinity lakes (Borgmann, 1983; LaZerte, 1984). Therefore, it seems unlikely that metal concentrations alone or the joint action of hydrogen ions and metals are lethal to mollusks in the acidifying lakes of southern Ontario, Canada.

Other metals, such as copper, mercury, and silver, are also toxic to mollusks (Wurtz, 1962), but their toxicity in acidifying lakes has not yet been investigated. Heavy metal toxicity is affected by hardness and pH (Wurtz, 1962; Arthur and Leonard, 1970) and is a major factor in the disappearance of mollusks below acid-mine drainages and industrial-waste outfalls [Mullican *et al.*, 1960 (*vide* Fuller, 1974); Cairns *et al.*, 1971 (*vide* Harman, 1974); Imlay, 1971; Yokley, 1973]. While the levels of many metals are elevated in acid precipitation (Jeffries and Snyder, 1981; Galloway *et al.*, 1983) and in most acidifying lakes (Schindler *et al.*, 1980; Forstner and Wittmann, 1983; Luoma, 1983), studies on the toxicity of metal mixtures to mollusks, such as those done by Hutchinson and Sprague (1986) on fish, remain to be done.

INDIRECT EFFECTS

POPULATION LEVEL

The most significant effects of acidifying environments on populations of freshwater mollusks are changes in shell composition, shell morphology, reproduction, and growth. There are probably other indirect effects but only these have been reported to date and are elaborated upon below.

The changes in shell composition of mollusks in relation to the buffering capacity of the water have been determined from simple correlations between calcium content of the shell and the alkalinity and pH of the water (Mackie and Flippance, 1983c); Table 2 shows which species exhibit these significant correlations. As might be expected, most species [e.g. *Physella gyrina* (Say), *Cincinnatia cincinnatiensis* (Anthony), *Pisidium casertanum*, *P. compressum*, *Sphaerium striatinum*, *Anodonta grandis* Say, and *E. complanata* (Lightfoot)] show decreasing calcium content of the animal with decreasing alkalinity (i.e. positive correlations). Only one species studied, *Sphaerium rhomboideum* (Say), showed a

Table 2. Summary of significant ($P < 0.05$) correlations between calcium content of freshwater mollusks and pH and alkalinity of the water. Table is based on data given in Mackie and Flippance (1983c). + indicates a positive correlation, - indicates a negative correlation, and o indicates no significant correlation ($P > 0.05$).

GASTROPOD SPECIES	CORRELATION		BIVALVE SPECIES	CORRELATION	
	pH	Alk.		pH	Alk.
<i>Physella gyrina</i>	o	+	<i>Musculium securis</i>	o	o
<i>Helisoma anceps</i>	o	o	<i>Pisidium casertanum</i>	+	+
<i>Gyraulus parvus</i>	+	o	<i>Pisidium compressum</i>	-	+
<i>Amnicola limosa</i>	o	o	<i>Pisidium variable</i>	o	o
<i>Cincinnatia cincinnatiensis</i>	+	+	<i>Sphaerium rhomboideum</i>	-	-
<i>Valvata tricarinata</i>	-	o	<i>Sphaerium simile</i>	-	o
<i>Campeloma decisum</i>	o	o	<i>Sphaerium striatinum</i>	+	+
			<i>Anodonta grandis</i>	+	+
			<i>Elliptio complanata</i>	+	+
			<i>Lampsilis radiata</i>	o	o
			(Gmelin, 1792)		

significant negative correlation indicating that as alkalinity decreases, the calcium content of the animal increases. However, this species is found only in waters with alkalinities greater than about 40 mg $\text{CaCO}_3 \text{ l}^{-1}$. Most species in Table 2 also show a significant positive correlation with pH; those species that show negative correlations are without exception characteristic of high alkalinity environments.

There is also some evidence that certain species of mollusks have greater amounts of carbon in their shells than other species in acidifying lakes (Mackie et al., 1983). Table 3 shows the carbon content of the shell of several species from neutral (near pH 7) lakes. It is interesting to note that the most sensitive species in the list (*Sphaerium striatinum*) has the least amount of carbon and the most tolerant (*Pisidium casertanum*) has the most carbon in the shell.

Among the most interesting effects are the changes that occur in shell morphology, as detected in canonical cor-

relation analyses (Mackie and Flippance, 1983a). The most significant canonical variates ($P < 0.0001$) indicate that a shortening of the shell with an increase in calcium content and total weight is related to decreasing alkalinity and pH in relation to calcium and total hardness for *Valvata tricarinata*, *Campeloma decisum* (Say), *Pisidium casertanum*, and *P. variable* Prime (Fig. 3). For *Amnicola limosa*, *Sphaerium simile* (Say), and *S. striatinum*, the shortening of the shell and an increase in calcium content and total weight is related to decreasing alkalinity and calcium hardness relative to total hardness; pH is less important as a variable. Only three species [*Helisoma anceps* (Menke), *M. securis* and *P. compressum*] of fifteen studied showed increasing shell size without changes in shell weight as alkalinity increased in relation to calcium or total hardness. Within the Unionidae, shorter, heavier shells in *Elliptio complanata* are related to increasing alkalinity, total hardness, and pH relative to calcium hardness. In *A. grandis*, shorter, heavier shells are related to decreasing alkalinity relative to total hardness; calcium hardness and pH seem less important.

The canonical correlation analyses of Mackie and Flippance (1983a) also indicate that acidifying environments have different effects on different species of mollusks. In many species (e.g. *Amnicola limosa*, *Valvata tricarinata*, *Campeloma decisum*, *Pisidium casertanum*, *P. variable*, *Sphaerium simile*, *S. striatinum*, *Amnicola grandis*, and *Elliptio complanata*) a high density of calcium carbonate can be maintained in the shell by forming shorter, heavier shells. Hence, the protection offered by the calcareous shell is maintained. The only difference among the species is the factor or set of factors that seem to be related to these changes. For all but *E. complanata* the shorter, heavier shell may be considered a defensive mechanism since it is observed in waters with decreasing alkalinity, pH or calcium hardness. The only species that can afford long, thin shells are those that are characteristically found in high-alkalinity water (e.g. *P. compressum*). Such species appear to have no defensive mechanisms for decreasing alkalinity and are eliminated from

Table 3. Calcium carbonate and carbon content of shells in common species of freshwater mollusks. The species are arranged in order of decreasing calcium carbonate content. 95% confidence intervals are given in parentheses. N.D. denotes that carbon content was not determined.

SPECIES	Shell CaCO_3 as % of total dry wt.	$\mu\text{g C mg}^{-1}$ shell
<i>Elliptio complanata</i>	93.3 (3.51)	7.68 (2.41)
<i>Sphaerium striatinum</i>	92.2 (1.69)	5.33 (0.68)
<i>Sphaerium simile</i>	90.7 (2.53)	N.D.
<i>Pisidium compressum</i>	90.3 (0.89)	N.D.
<i>Anodonta grandis</i>	90.1 (4.08)	N.D.
<i>Campeloma decisum</i>	89.6 (1.44)	8.24 (2.01)
<i>Amnicola limosa</i>	88.7 (3.00)	6.11 (1.02)
<i>Valvata tricarinata</i>	88.0 (0.92)	N.D.
<i>Helisoma anceps</i>	80.8 (1.75)	N.D.
<i>Physella gyrina</i>	80.6 (2.68)	7.33 (1.33)
<i>Musculium securis</i>	80.0 (3.21)	8.32 (1.57)
<i>Pisidium casertanum</i>	65.8 (1.66)	10.18 (2.77)

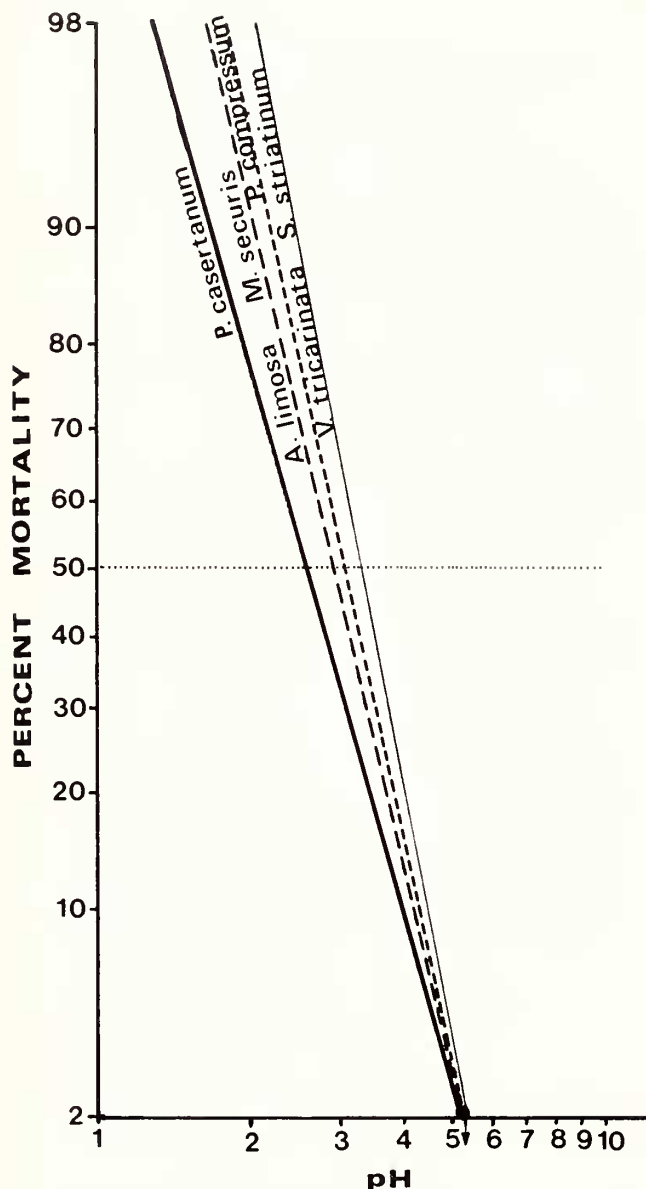


Fig. 2. 96 hr LC50 plots for pH for six species of freshwater mollusks in static laboratory bioassays. Data are from Mackie (1986).

waters with alkalinities less than about 20 mg $\text{CaCO}_3 \text{ l}^{-1}$. *E. complanata* exhibits another type of response where the shell becomes increasingly thinner as acidification proceeds. In fact, some populations in low-alkalinity lakes of southern Ontario have such thin shells that they are difficult to pick up without pushing the fingers through the shell. It is possible that dissolution of calcium carbonate from the shell may be buffering the excess hydrogen ions within the internal milieu of the clam.

Perhaps the most significant effect of decreasing pH and alkalinities is the decreased reproductive capacities of mollusks. Rooke and Mackie (1984c) reported reduced production of eggs and extramarsupial larvae in *Amnicola limosa*

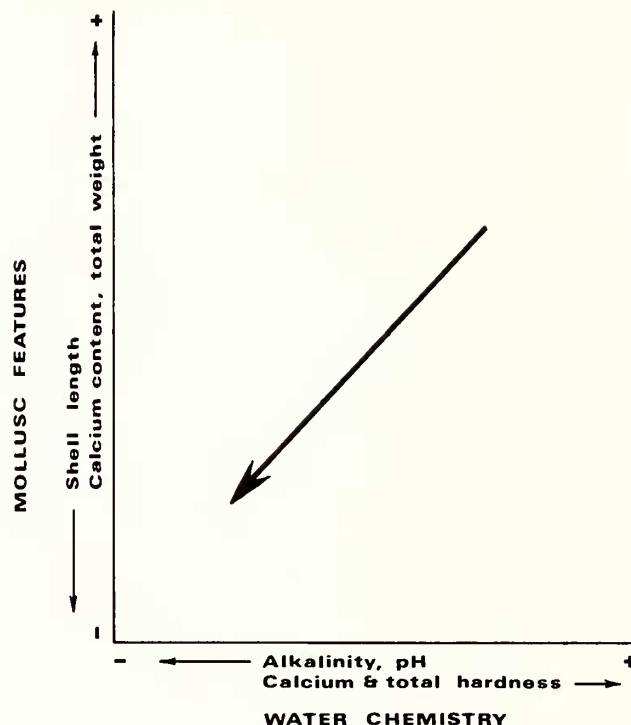


Fig. 3. Summary of the most common significant canonical correlation for the first canonical variate on data reported by Mackie and Flippance (1983a). The graph shows that shell length tended to decrease relative to calcium content and total weight of the species examined (see text) as the pH and alkalinity decreased relative to the calcium and total hardness of the water.

and *Pisidium casertanum* in lakes with total alkalinities below 1 mg $\text{CaCO}_3 \text{ l}^{-1}$ (Fig. 4).

An equally significant effect is the impaired development of eggs at low pH. Servos *et al.* (1984) reported impaired development of eggs of *A. limosa* in the laboratory at and below pH 5.0 and delayed development at pH 5.5 relative to pH 6.0 (Fig. 5); they also reported slightly reduced natalities in *Pisidium casertanum* and *P. ferrugineum* Prime in low-alkalinity lakes relative to higher-alkalinity lakes.

There is also good evidence that the growth of some mollusks are affected in low-alkalinity lakes. Rooke and Mackie (1984c) found that the growth rates of *Amnicola limosa* were greatest in high-alkalinity lakes ($0.013 \text{ mm day}^{-1}$) and least in low-alkalinity lakes ($0.008 \text{ mm day}^{-1}$). However, in the same study Rooke and Mackie were unable to show any effects of low-alkalinity environments on the growth of *Pisidium casertanum* or *P. ferrugineum*.

COMMUNITY LEVEL

The above results clearly indicate that acidic environments are affecting the biology of freshwater mollusk populations. These effects differ for each species of mollusk but ultimately one can expect to observe declines in production and diversity as lakes acidify. This has been observed

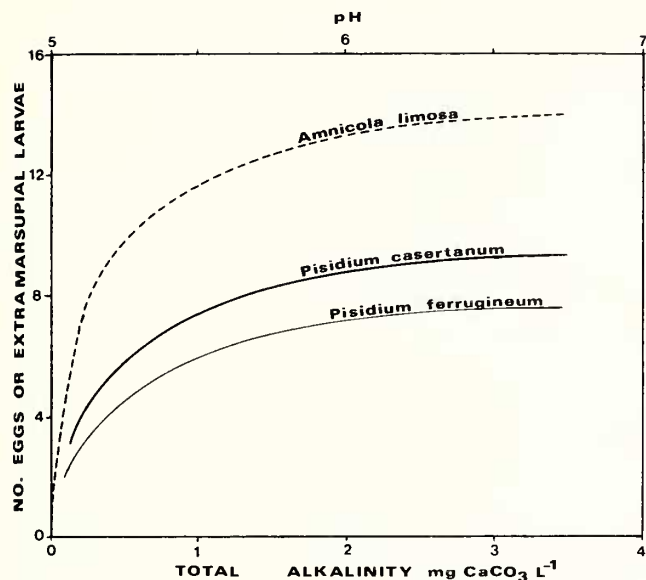


Fig. 4. Trends in natalities of three species of mollusks common in low-alkalinity lakes in south-central Ontario. Curves are based on data reported by Servos *et al.* (1985).

in low-alkalinity lakes of southern Ontario, Canada (Figs. 6, 7). Rooke and Mackie (1984c) reported greater levels of annual production of *Amnicola limosa* in higher alkalinity lakes ($70 - 80 \text{ mg m}^{-2}$) than in low-alkalinity lakes ($0 - 26 \text{ mg m}^{-2}$). However, the annual production of some species of Pisidiidae (*Pisidium casertanum*, *P. ferrugineum*) appeared to be similar

between low- and high-alkalinity lakes. Nevertheless, the annual production of other pisidiids (including *P. compressum*, *P. variabile*, and *Sphaerium striatinum*) must be affected because they are not found in low-alkalinity lakes.

Using data in Mackie and Flippance (1983c), figure 7 shows extremely large variations in the numbers of species of freshwater mollusks in lakes with high alkalinities (greater than about $20 \text{ mg CaCO}_3 \text{ l}^{-1}$). Hence, factors other than pH and alkalinity seem to affect the diversity of mollusks in environments with alkalinities exceeding about $20 \text{ mg CaCO}_3 \text{ l}^{-1}$, but below this value, pH and alkalinity explain a large part of the variation in diversity. Harman and Berg (1971), Harrel and Dorris (1968), Harrison *et al.* (1970), and Houpp (1970) have all reported direct correlations between alkalinity and production and diversity of mollusks, but all studies were done on waters with alkalinities exceeding $20 \text{ mg CaCO}_3 \text{ l}^{-1}$. Hunter (1964) claims that calcium is a better predictor of species diversity; waters with $> 25 \text{ mg Ca l}^{-1}$ can support all molluscan species in a geographic region, waters with 10 to 25 mg Ca l^{-1} can support 55%, waters with 5 to 10 mg Ca l^{-1} can support about 40%, and waters with $< 3 \text{ mg Ca l}^{-1}$ support less than 5%.

Finally, the type of faunal community also seems to be affected. The community appears to change from one containing a large proportion of epifaunal grazers (e.g. gastropods) to infaunal filter feeders (e.g. Pisidiidae). The organisms that survive the longest in low-alkalinity lakes appear to be those that are associated with the sediments, perhaps because the sediments have a greater capacity to buffer additions of hydrogen ions than does the water.

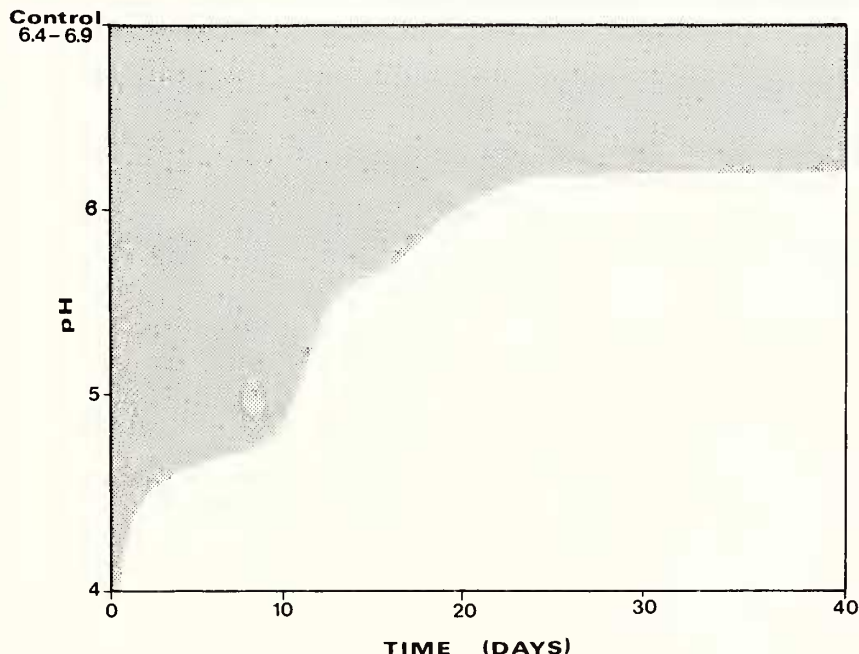


Fig. 5. Graph to show the times at which eggs of *Amnicola limosa* kept at different pH's fail to keep pace with eggs kept at pH 6.4 to 6.9 (i.e. control) (e.g. eggs kept at pH 5 are at the same stage of development as the control eggs for up to 10 days, after which eggs at pH 5 fail to develop). Graph is based on data in Servos *et al.* (1985).

LAKE RESPONSES

Since mollusks contain such large amounts of calcium carbonate in their bodies (namely the shell) one would expect that mollusks can provide a source or carbonate for the buffer systems of acidifying lakes. If molluscan carbonates are formed from carbon dioxide there must be a concomitant release of acid because the negative carbonate ion cannot be formed from neutral carbon dioxide without the liberation of protons. Mollusks should, therefore, produce acid during the process of shell formation, above and beyond that for any heterotrophic organism. Once the mollusks die the synthesized carbonates should be released and contribute to the carbonate pool of the environment. Hence, mollusks can play a role in the sources, cycling, and storage of carbonates. These conclusions are supported by the studies of Rooke and Mackie (1984b) who used a series of aquaria containing various combinations of water, sediment, and mollusks to investigate the effects of mollusks on the alkalinity of the water. They found that live mollusks acidified the water and dead, decomposing mollusks were associated with an increase in alkalinity. Aquaria containing dead mollusks had more stable alkalinity concentrations than aquaria with burrowers, or aquaria with just sediments and water when all received additions of "acid rain" (pH 4.1). Non-molluscan invertebrates liberated acid-neutralizing materials from the sediments but the source was quickly depleted. These general trends are depicted in figure 8.

Similar experiments were also performed in the field under more natural conditions, using a trough system (Mackie *et al.*, 1983). The trough was divided into three channels; one was treated with limestone, one was treated with unionid

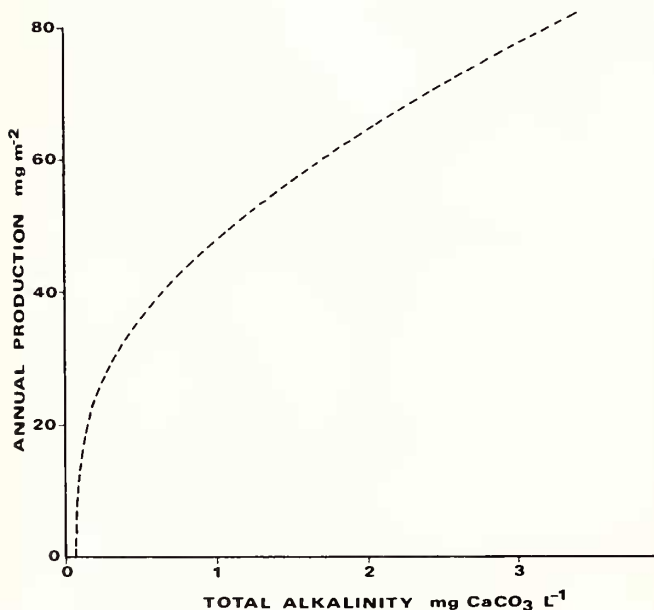


Fig. 6. Annual production of *Amnicola limosa* in relation to total alkalinity of the environment. Based on data in Rooke and Mackie (1984c).

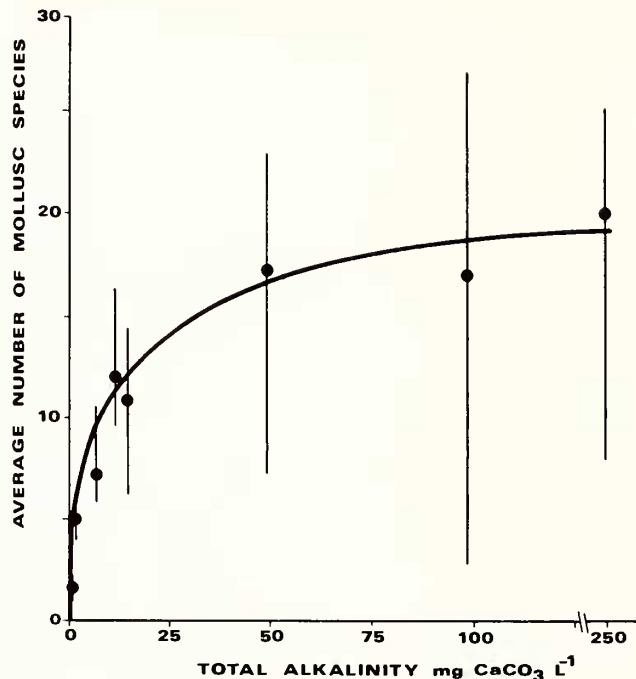


Fig. 7. Average number of mollusk species in relation to the total alkalinity of the environment. Data are from Mackie and Flippance (1983c).

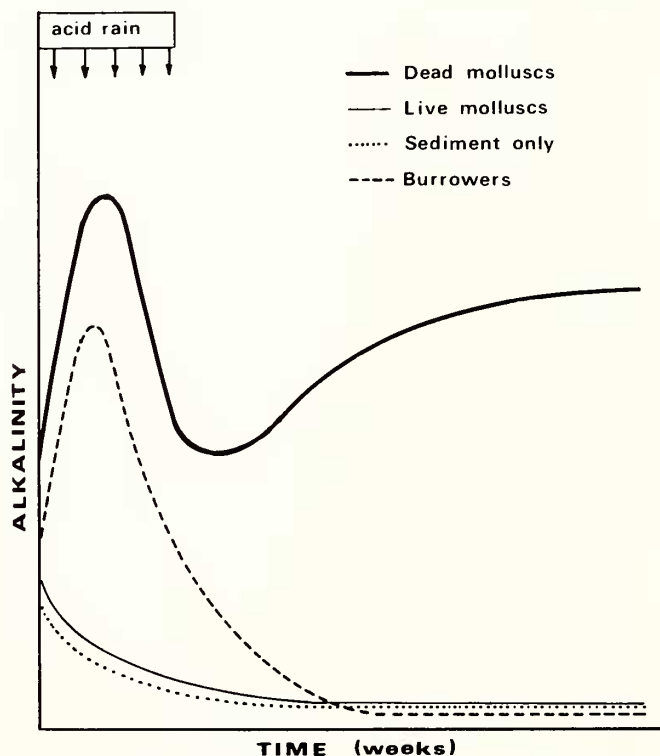


Fig. 8. Changes in alkalinities in aquaria containing either dead mollusks, live mollusks, sediment only, or burrowing dragonflies (*Gomphus*) and mayflies (*Ephemera*). Based on data in Rooke and Mackie (1984b).

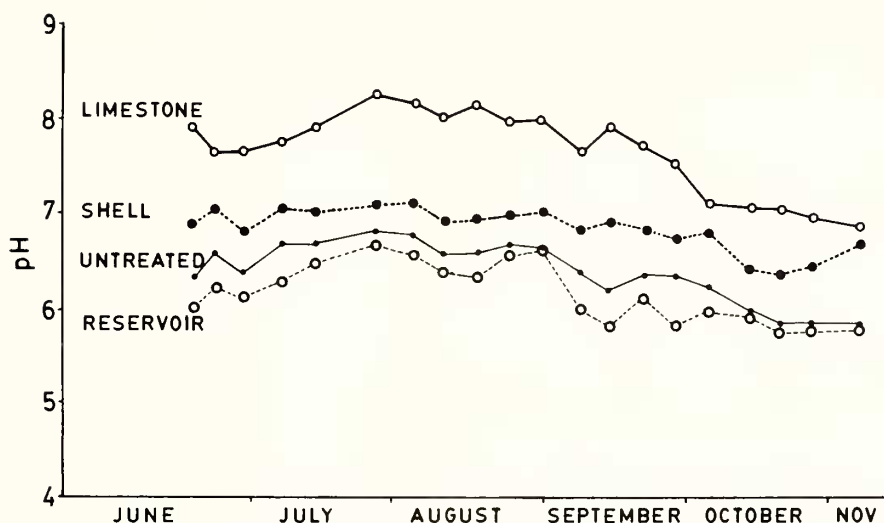


Fig. 9. Changes in pH over time in troughs containing either limestone, shells of *Elliptio complanata*, or no buffering material (untreated) using water from the outflow of Plastic Lake in south-central Ontario. The reservoir held water to maintain a pressure head before passing through the troughs. See Mackie et al. (1983) for details.

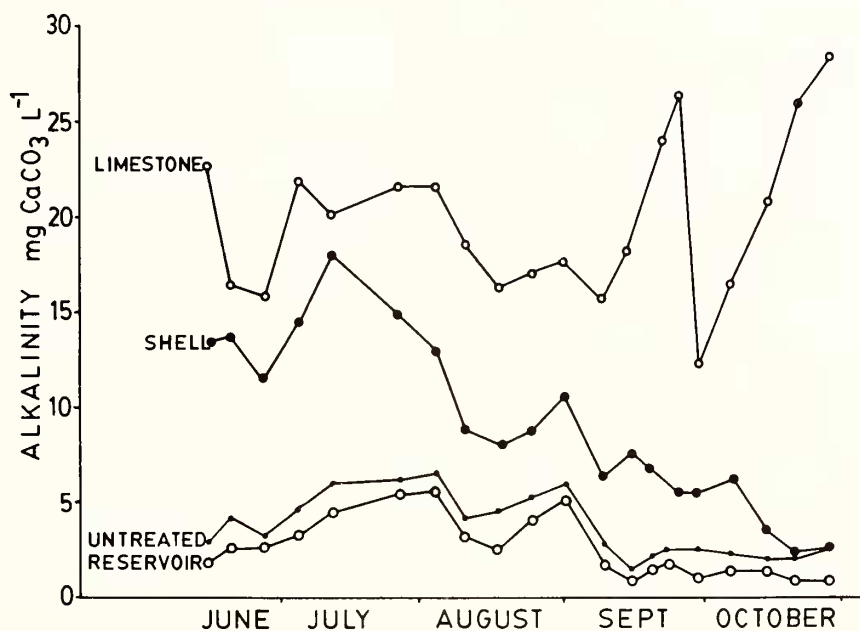


Fig. 10. Changes in alkalinities over time in troughs containing the same materials described for figure 9.

(*Elliptio complanata*) shells, and the third was untreated (i.e. control). The unionids were shucked and only the separated valves (with some remnants of adductor muscles attached) were used. Water from the outflow of Plastic Lake, an acidifying lake in south-central Ontario, was allowed to flow through the trough system and the changes in pH and alkalinity were recorded over time. Figures 9 and 10 show that the mollusk shells contributed some alkalinity but not as much as the limestone. Also, the limestone maintained a higher alkalinity than the mollusk shells after five months, even though there was still 90% of the calcareous shell material

remaining. Shell dissolution could have been inhibited by the several layers of conchiolin that separate the nacreous layers of calcium carbonate. From this point of view, it could have been better to use shells of Corbiculacea species [e.g. *Corbicula fluminea* (Müller)] which lack internal conchiolin layers and dissolve more readily in acidic solutions (Kat, 1982). Moreover, the ammonia levels in the trough with mollusk shells rose to extremely high levels in the first few weeks of the experiment (Fig. 11), probably due to the breakdown of protein and ammonification of amino acids originating from residual adductor muscles on the inner valves of the shells.

The conchiolin layers could also have contributed to the ammonia levels.

CONCLUSIONS

In conclusion, the levels of hydrogen ions and metals in most acidifying lakes of southern Ontario are not great enough to directly eliminate the mollusks, but the present levels appear to be causing changes in shell composition, shell morphology, reproduction and growth that are sufficient to cause decreased production and diversity, and a change from a greater proportion of epifaunal grazers to infaunal, filter feeding mollusk communities.

ACKNOWLEDGMENTS

The study was supported by the National Science Engineering Research Council of Canada, Grant No. A9882. I am grateful to the anonymous referees for making suggestions that greatly improved the manuscript.

LITERATURE CITED

- Arthur, J. W. and E. N. Leonard. 1980. Effects of copper on *Gammarus pseudolimnaeus*, *Campeloma decisum*, and *Physa integra* in soft water. *Journal of the Fisheries Research Board of Canada* 27:1277-1283.
- Borgmann, U. 1983. Metal speciation and toxicity of free metal ions to aquatic biota. In: *Offprints From Aquatic Toxicology*, J. O. Nriagu, ed. pp. 47-72. John Wiley and Sons, Toronto, Canada.
- Buckley, D. E. 1977. The distribution and ecology of the molluscan fauna of the Black River drainage basin in northern New York. Master's Thesis. State University College at Oneonta, New York, 276 pp.
- Cairns, J., J. S. Crossman, K. L. Dickson and E. E. Herricks. 1971. The recovery of damaged streams. *Associated Southeastern Biological Bulletin* 18:49-106.
- Forstner, U. and G. T. W. Wittmann. 1983. *Metal Pollution in the Aquatic Environment*. Springer-Verlag. 486 pp.
- Fuller, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia). In: *Pollution Ecology of Freshwater Invertebrates*. C. W. Hart Jr. and S. L. H. Fuller, eds. pp. 215-273. Academic Press, New York.
- Galloway, J. N., J. D. Thornton, S. A. Norton, H. L. Volchok and R. A. N. Mclean. 1982. Trace metals in atmospheric deposition: A review and assessment. *The Atmospheric Environment* 16:1677-1700.
- Harman, W. N. 1969. The effect of changing pH on the Unionidae. *The Nautilus* 83:69-70.
- Harman, W. N. 1974. Snails (Mollusca: Gastropoda). In: *Pollution ecology of freshwater invertebrates*. C. W. Hart Jr. and S. L. H. Fuller, eds. pp. 275-312. Academic Press, New York.
- Harman, W. N. and C. O. Berg. 1971. The freshwater Gastropod of central New York with illustrated keys to the genera and species. *Search Agriculture* 1:1-68.
- Harrel, R. C. and T. C. Dorris. 1968. Stream order, morphometry, physicochemical conditions and community structure of benthic macroinvertebrates in an intermittent stream system. *American Midland Naturalist* 80:220-251.
- Harrison, A. D., N. V. Williams and G. Grieg. 1970. Studies on the effect of calcium bicarbonate concentrations on the biology of *Biomphalaria pfeifferi* (Krauss) (Gastropoda: Pulmonata). *Hydrobiologia* 36:317-327.
- Houp, K. H. 1970. Population dynamics of *Pleurocera acuta* in a central Kentucky limestone stream. *American Midland Naturalist* 83:81-88.
- Hunter, W. R. 1964. Physiological aspects of ecology in non-marine molluscs. In: *Physiology of Mollusca*. K. M. Wilbur and C. M. Yonge, eds. pp. 83-116. Academic Press, New York.
- Hutchinson, N. J. and J. B. Sprague. 1986. Toxicity of trace metal mixtures to American flagfish (*Jordanella floridae*) in soft, acidic water and implications for culture acidification. *Canadian Journal of Fisheries and Aquatic Sciences* 43:647-655.
- Imlay, M. J. 1971. Bioassay tests with naiads. In: *Proceedings of a Symposium on Rare and Endangered Mollusks (Naiads) of the U.S.* S. E. Jorgensen and R. W. Sharp, eds. pp. 1-79. United

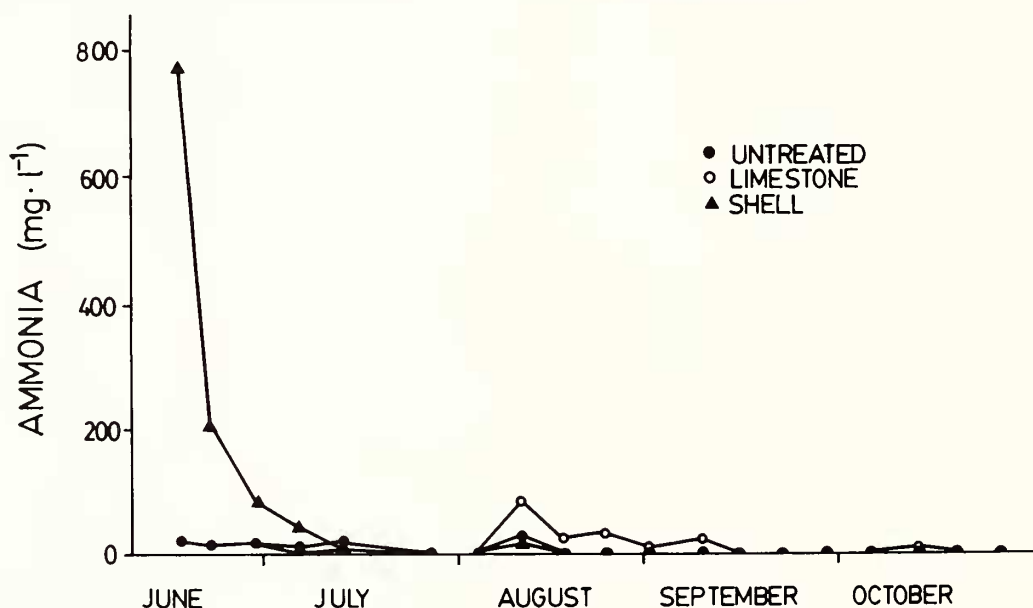


Fig. 11. Changes in ammonia concentrations over time in troughs containing the same materials described for figure 9.

- States Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife.
- Jeffries, D. S. and W. R. Snyder. 1981. Atmospheric deposition of heavy metals in central Ontario. *Water, Air, and Soil Pollution* 15:127-152.
- Jewell, M. E. 1922. The fauna of an acid stream. *Ecology* 3:22-28.
- Kat, P. W. 1982. Shell dissolution as a significant cause of mortality for *Corbicula fluminea* (Bivalvia: Corbiculidae) inhabiting acidic waters. *Malacological Review* 15:129-134.
- LaZerte, B. D. 1984. Forms of aqueous aluminum in acidified catchments of central Ontario: a methodological analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 41:766-776.
- Luoma, S. N. 1983. Bioavailability of trace metals to aquatic organisms - a review. *Science of the Total Environment* 28:1-22.
- Mackie, G. L. 1986. Tolerances of five benthic invertebrates to hydrogen ions and metals (Cd, Pb, Al). *Environmental Pollution* (in review).
- Mackie, G. L. and L. A. Flippance. 1983a. Relationships between buffering capacity of water and the size and calcium content of freshwater mollusks. *Freshwater Invertebrate Biology* 2:48-55.
- Mackie, G. L. and L. A. Flippance. 1983b. Calcium sources for growth of *Musculium securis* (Bivalvia: Pisidiidae). *Canadian Journal of Zoology* 61:874-878.
- Mackie, G. L. and L. A. Flippance. 1983c. Intra- and interspecific variations in calcium content of freshwater Mollusca in relation to calcium content of the water. *Journal of Molluscan Studies* 49:204-212.
- Mackie, G. L., J. B. Rooke, and M. R. Servos. 1983. *Cause and Effect Relationships Between Mollusca and Acid-Neutralizing Capacity of Acidifying Lakes*. Report to the National Research Council of Canada, NRCC Associate Committee on Scientific Criteria for Environmental Quality, Ottawa, Ontario, Canada. 260 p.
- Matteson, M. R. 1955. Studies on the natural history of the Unionidae. *American Midland Naturalist* 53:126-145.
- Morrison, J. P. E. 1932. A report on the Mollusca of the northeastern Wisconsin Lake district. *Transactions of the Wisconsin Academy of Science, Arts and Letters* 27:359-396.
- Mullican, H. N., R. M. Sinclair and B. G. Isom. 1960. *Survey of the Aquatic Biota of the Nolichucky River in the State of Tennessee*. Tennessee Stream Pollution Control Board, Nashville. 28 pp.
- Økland, J. 1969. Distribution and ecology of the fresh-water snails (Gastropoda) of Norway. *Malacologia* 9:143-151.
- Økland, J. 1980. Environment and snails (Gastropoda): Studies of 1000 lakes in Norway. In: *Proceedings of the International Conference on the Ecological Impact of Acid Precipitation*. D. Drablos and A. Tollan, eds. pp. 322-323. Norway.
- Økland, J. and J. G. J. Kuiper. 1980. *Small Mussels (Sphaeriidae) in Fresh Water in Norway - Distribution, Ecology, and Relation to Acidification of Lakes*. SNSF Project Oslo-As, Norway, International Report 61/80.
- Økland, J. and K. A. Økland. 1980. pH level and food organisms for fish; studies of 1000 lakes in Norway. In: *Proceedings of the International Conference on the Ecological Impact of Acid Precipitation*. D. Drablos and A. Tollan, eds. pp. 326-327. Norway, 1980, SNSF Project.
- Økland, K. A. 1979. Sphaeriidae of Norway: A project of studying ecological requirements and geographical distribution. *Malacologia* 18:223-226.
- Økland, K. A. 1980. Mussels and crustaceans: Studies of 1000 lakes in Norway. In: *Proceedings of the International Conference on the Ecological Impact of Acid Precipitation*. D. Drablos and A. Tollan, eds. pp. 324-325. Norway.
- Rooke, J. B. and G. L. Mackie. 1984a. Mollusca of six low-alkalinity lakes in Ontario. *Ontario Journal of Fisheries and Aquatic Sciences* 41:777-782.
- Rooke, J. B. and G. L. Mackie. 1984b. Laboratory studies of the effects of the Mollusca on alkalinity of their freshwater environment. *Canadian Journal of Zoology* 62:793-797.
- Rooke, J. B. and G. L. Mackie. 1984c. Growth and production of three species of molluscs in six low-alkalinity lakes in Ontario, Canada. *Canadian Journal of Zoology* 62:1474-1478.
- Schindler, D. W., R. H. Hesslein, R. Wagemann and W. A. Broeker. 1980. Effects of acidification on mobilization of heavy metals and radionuclides from the sediments of the freshwater lake. *Canadian Journal of Fisheries and Aquatic Sciences* 37:373-377.
- Servos, M. R. 1983. The effect of short- and long-term acidification on selected molluscs of south-central Ontario. Master's Thesis, University of Guelph, Guelph, Ontario. 112 pp.
- Servos, M. R., J. B. Rooke, and G. L. Mackie. 1985. Reproduction of selected Mollusca in some low-alkalinity lakes in south-central Ontario. *Canadian Journal of Zoology* 63:511-515.
- Wurtz, C. B. 1962. Zinc effects on fresh-water mollusks. *The Nautilus* 76:53-61.
- Yokley, P., Jr. 1973. *Freshwater mussel ecology, Kentucky Lake, Tennessee*. Project 4-46-R, Tennessee Game and Fish Commission, Nashville, 133 pp.